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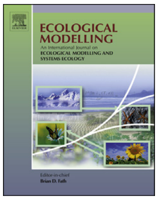

# Dispersal and climate warming determine range shift in model reptile populations

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## ABSTRACT

Average air temperature is predicted to rise by at least 3 °C across the 21st century. As individual sex (male or female) is determined by temperature in many reptiles, there are concerns that climate warming will skew offspring sex ratios and local species extinctions will follow. Range shift away from hotter areas through dispersal may prevent species extinctions in many reptiles with temperature-dependent sex determination (TSD), and could be facilitated or impeded by sex-biased populations at the expanding edge. We used a simulation model to examine the role of sex-determining mechanism [TSD and genotypic sex determination (GSD)], climate warming and dispersal in determining range shift and population growth in reptiles. Dispersal influenced range shift (after climate warming) in TSD species to a greater extent than in GSD species. Our novel finding is that biased sex ratios may influence range shift, through the mixing of the rare sex (females) with males located at the colder range edges, as both sexes disperse. However, if faced with climate warming of 3 °C over the next 100 years many TSD reptiles will show limited capacity for range shift.

## 1. Introduction

Global average air temperature has increased by approximately 0.8 °C during the 20th century and is predicted to rise an additional 2 to 6 °C during the 21st century (IPCC, 2013). Reptiles with temperature-dependent sex determination (TSD) are considered to be especially vulnerable to climate warming as offspring sex ratios are determined by temperature. There have been numerous predictions that warming climates will skew offspring sex ratios towards females, resulting in local population extinctions, in the absence of dispersal or in situ changes in nesting behaviour (Grayson et al., 2014; Hawkes et al., 2007; Hawkes et al., 2009; Hays et al., 2003; Janzen, 1994; Witt et al., 2010). In the tuatara climate warming may skew the sex ratio towards males resulting in local population declines or extinctions (Mitchell et al., 2008). However, TSD reptiles have existed for hundreds of millions of years and persisted despite historical climatic changes involving both warming and cooling (Silber et al., 2011). To elaborate, if projections of around 6 °C are reached in the 21st century, then the Earth will have reached the same amount of mean global warming as it did following a period of around 5000 years at the end of the last glacial maximum (IPCC, 2013).

One potential advantage of climate warming for TSD reptiles is the creation of more favourable microclimates in areas that were unfavourable. Changes in habitat favourability may allow species to shift or expand their geographical ranges in cooler latitudes, and in warmer latitudes altitudinal shifts may occur (Hughes, 2003; Parmesan et al., 2000). Hence, population growth may occur if colonisation of the expanded range is successful. However, range expansion relies on the ability of a species to successfully disperse, and many TSD reptiles are thought to be poor dispersers (Escobedo-Galvan et al., 2011). Furthermore, some terrestrial (Olsson and Shine, 2003) and aquatic (Brown and Brooks, 1993; Mockford et al., 2005; Morreale et al., 1984) reptiles only disperse short distances.

In addition to the importance of dispersal distances for range expansion, the sex of the dispersers may be crucially important for TSD populations at range edges (Boyle et al., 2014a). Kallimanis (2010) proposed a model describing the geographical distribution of sex ratios in TSD reptiles, and their importance for range boundaries. In this model, unbalanced sex ratios in marginal habitats are assumed to limit population growth and set the limit of range expansion under stable climatic conditions. The sex ratios of TSD reptiles vary with geography, with balanced sex ratios occurring in the core regions, and male- or female-biased sex ratios at the edges or limits of thermal ranges (Kallimanis, 2010). Under warming

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scenarios, the ‘leading’ (colder) edges of ranges are environments of historically low temperatures containing male-biased sex ratios, and the ‘trailing’ (warmer) edges are environments of high temperatures with female-biased sex ratios. Kallimanis (2010) argued for TSD pattern 1A that at the colder edge, warming climates will change sex ratios from male biased to even (1:1), and population growth will increase, producing a ‘pool’ of dispersers to expand their ranges into previously cooler areas. Conversely, the warmer edge populations will become extinct as ranges become even hotter and sex ratios reach 100% female bias (Escobedo-Galvan et al., 2011; Kallimanis, 2010).

Spatial variation in sex ratios may not occur as over time the increased population sizes that occur as a result of biased sex ratios would disappear as frequency dependent selection favours unbiased sex ratios by allowing adaptation to local temperatures (Fisher, 1930). Morjan (2003) and McGaugh and Janzen (2011) demonstrated that the heritability of sex determining factors enables sex determining mechanisms and maternal behaviour to adapt to local temperatures. This adaptation would in principle reduce the relationship between geography and local population sex ratios. However, Morjan (2003) allowed the pivotal temperature (the temperature at which male and female offspring are produced in 50:50 sex ratios) to evolve to any temperature, but in natural systems the pivotal temperature varies little between populations (Harts et al., 2014). Harts et al. (2014) demonstrated that local adaptation in pivotal temperature is limited by demographic dominance in females.

Furthermore there are several empirical studies suggesting sex ratios do not vary spatially over time. Escobedo-Galvan et al. (2011) argue that variation in local temperature is uncorrelated with offspring sex ratio in species with TSD 1A and II. Gibbons et al. (1988) that TSD species with wide variation in mean ambient temperatures [e.g. common snapping turtles (*Chelydra serpentina*) and painted turtles (*Chrysemys picta*)] show no latitudinal trends in population sex ratios. However, there is still relatively little empirical evidence to support the absence of sex ratio patterns across geographical ranges. Furthermore, there is considerable population variation in the sex-ratio of species described by Escobedo-Galvan et al. (2011) and these could be driven by variation in local climate.

There are two reasons to believe that population growth at the warm range margins could be enhanced by both female-biased sex ratios and by temperature-dependent increases in fitness. Demographic analyses have indicated that increases in reproduction and population growth are associated with female biased sex ratios, and not even sex ratios, as long as male density is not strongly limiting on female fecundity (Freedberg and Taylor, 2007). Moreover, higher temperatures have been shown to enhance the fitness of females in several lizard species (Warner and Shine, 2008; Holleley et al., 2015).

Notwithstanding, females at a warming range edge require males to fertilise their eggs. Dispersal by the rare sex is thought to be a driver of range limits in reptiles with TSD in stable climates (Boyle et al., 2014a). In many reptiles with TSD males are the rare sex and are more likely to disperse; thus, male recruitment through dispersal is thought to be essential to facilitate local population persistence in increasingly female-biased populations (Doody and Moore, 2011). However, other dispersal tendencies (i.e., female-biased or dispersal by both sexes) remain largely un-investigated. Sex-specific dispersal is more essential in maintaining populations of reptiles with TSD (through the mixing of the opposite sexes located towards either the warmer or colder range edges), than in reptiles with genotypic sex determination (GSD), in stable climates (Boyle et al., 2014a). To what extent will climate warming and dispersal determine the extent of range expansion in reptiles, and be more likely to lead to range expansion into previously cooler areas? In this paper, we develop a generalised model of reptiles with TSD (and GSD) distributed across a theoretical landscape to establish how sex-determining mechanisms, dispersal and climate warming determine the extent of range expansion. In Boyle et al. (2014b), we found that warmer climates producing female-biased sex ratios in model reptile populations with TSD resulted in larger female population sizes, but population size was reduced by male limitation on female fecundity. In Boyle et al. (2014a), we established the relationship between dispersal and sex determining mechanism on range limits in stable and not warming climates. Specifically, immigration of the rare sex into a sex-biased edge population can rescue the population from extinction. However, little is known of the role of dispersal by the rare sex in range expansion and population persistence as climates warm.

The aims of this paper are to extend these findings in order to (1) establish the relationship between climate warming, dispersal and sex-determining mechanism in driving range expansion in reptiles under climate change. TSD 1A (where females are produced at higher temperatures) is the model system; (2) examine the effects of warming climates (3 °C increase in temperature across 100 years) on population growth in reptiles. The model does not include evolutionary changes in demographic (birth and death) rates or the effects of temperature on sex ratios. This is an area for further study.

## 2. Materials and methods

### 2.1. Simulation model

A matrix (100 rows by 100 columns) of 10,000 populations was distributed across a continuous air temperature gradient, with each column assigned a temperature from 18 °C to 33 °C. Population range limits were measured by determining the proportion of populations that persist at each temperature. Each population in the matrix was initiated with 100 males and 100 females. We projected these populations for 1000 years under constant climate in a simulation to determine range limits under three different scenarios of dispersal, temperature-dependence of sex ratios and climate. The GSD scenarios were null models so that we could separate the effects of temperature-dependent sex ratio and survival on persistence and range expansion. Within each population, simulated population operations approximated logistic growth, including density-dependent juvenile survival (Boyle et al., 2014b).

Following the initial 1000-year range establishment, we projected 100 additional years under one of two climate scenarios: no climate change, and climate change. A 3 °C linear increase in ambient air temperature was selected as it is within the range of projected temperature increase across the 21st century (IPCC, 2013). Under the ‘no climate change’ scenario, the distribution of temperatures was maintained as 18 to 33 °C. Under the ‘climate change’ scenario, temperatures ranged from 18 to 33 °C for the first 1000 years. A 3 °C increase in temperatures across the final 100 years of the simulation (from 1000 to 1100 years) resulted in temperatures ranging from 21 to 36 °C, representing a new continuous temperature gradient.

### 2.2. Male limitation (B)

Individual female fecundity, $B$, was an integer that was sampled using a random binomial distribution based on the probability of fertilisation of a female, Pr{fert}, with a maximum value of $B_{\max}$:

$$B = B_{\max} \times Pr\{\text{fert}\} \tag{1}$$

Pr{fert}is a function of adult sex ratio (ASR), or the proportion of adults in the population that are male:

$$Pr\left\{\text{fert}\right\} = \frac{\text{ASR}}{\text{ASR} + b} \tag{2}$$

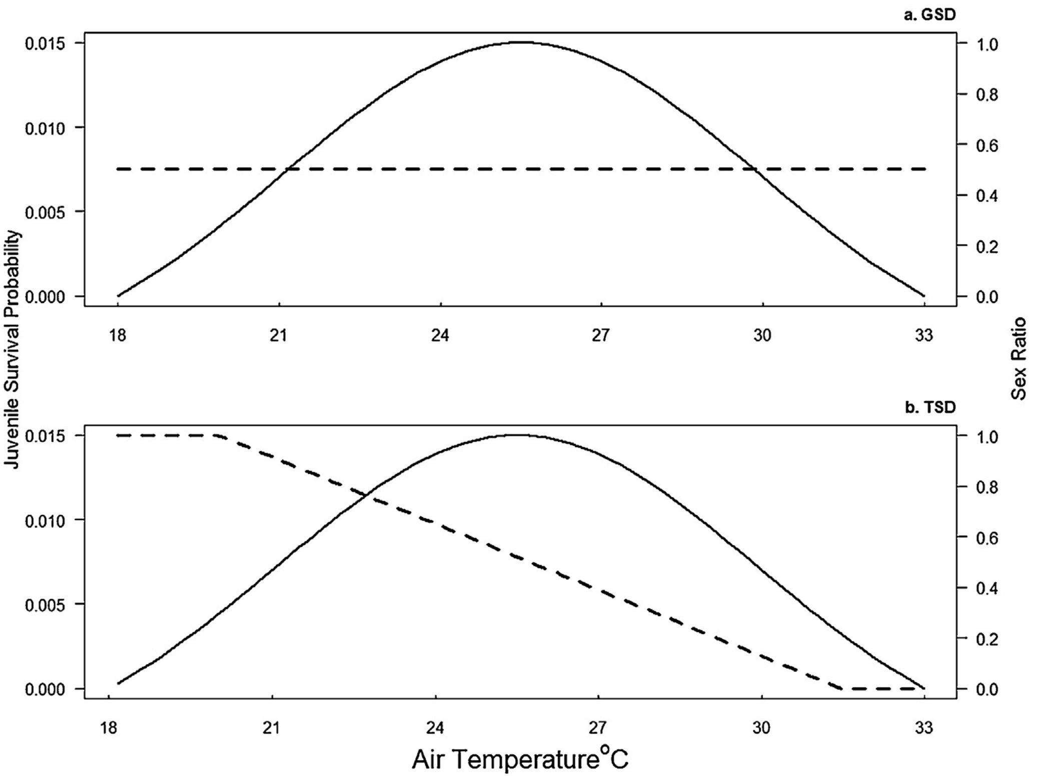

**Fig. 1.** Juvenile survival (solid line) and cohort sex ratio (dashed line) as a function of environmental temperature for (a) simulated GSD populations and (b) simulated TSD populations. Sex Ratio is the proportion of males; Juvenile Survival is after 1 year.

The shape parameter for Eq. (2), *b*, represents the relative strength of male limitation on female fecundity (Rankin and Kokko, 2007; Boyle et al., 2014b).

### 2.3. Cohort sex ratio (p)

Range limits were examined through two relationships between cohort sex ratio (CSR) and air temperature. The first cohort sex ratio (CSR) curve was flat, with the offspring sex ratio at 0.5 for all air temperatures, describing the pattern for a GSD species (slope $\beta = 0$ and intercept of $\alpha = 0.5$) (Fig. 1a, dashed line). CSR curve 2 represents a TSD species based upon the parameters derived for the painted turtle (Schwanz et al., 2010) with intercept $\alpha = 4.14$ and slope $\beta = -0.147$ (Fig. 1b, dashed line). The sex ratio produced for the long-term average air temperature for painted turtles is 0.6 (proportion of male offspring, Schwanz et al., 2010). Population size for stable air temperatures, *p* did not fluctuate across years (Boyle et al., 2014a).

### 2.4. Juvenile survival (a)

The number of surviving juveniles (males and females) was sampled using a random binomial distribution, based on the number of offspring produced and juvenile survival rate. Juvenile survival rate was density dependent, $ae^{-cN}$, where *N* is the total number of adult males and females in the population, *c* is the density-dependent constant ($c = 0.001$), and the baseline survival of juveniles (*a*) depended on temperature according to a normal distribution (the temperature-dependent embryonic survival (TS) curve) (Fig. 1a and b, solid line) (Boyle et al., 2014a).

The TS curve had a maximum baseline embryonic survival of $a_{\max} = 0.015$ (at 25 °C) and a minimum baseline survival value of zero. The range of temperatures that produced non-zero baseline juvenile survival probabilities was 18 to 33 °C. Survival rates are based on estimates from published values (Yntema and Mrosovsky, 1982).

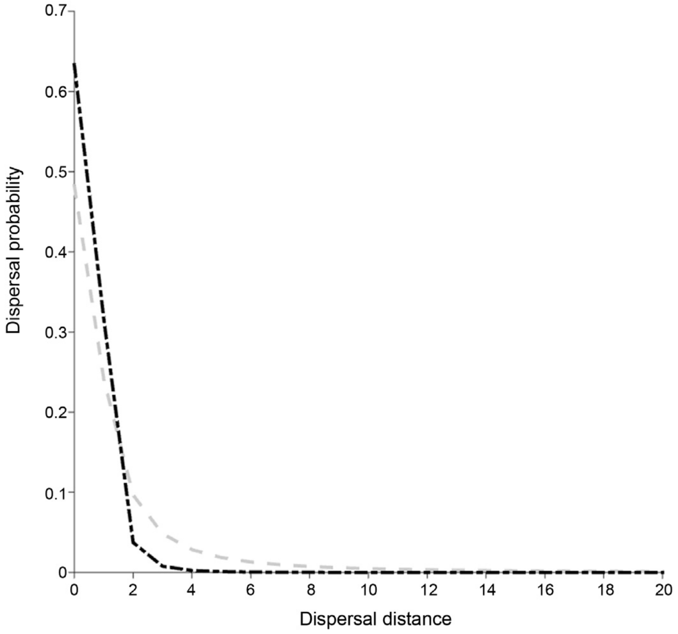

**Fig. 2.** Probability of an individual moving a certain number of cells (dispersal distance) across a population matrix for two fat-tailed dispersal kernels (Eq. (3)). Low dispersal (grey line) has parameters $A_L = 1$ and $Z_L = 2$, and very low dispersal (black line) has parameters $A_{VL} = 1$ and $Z_{VL} = 4$.

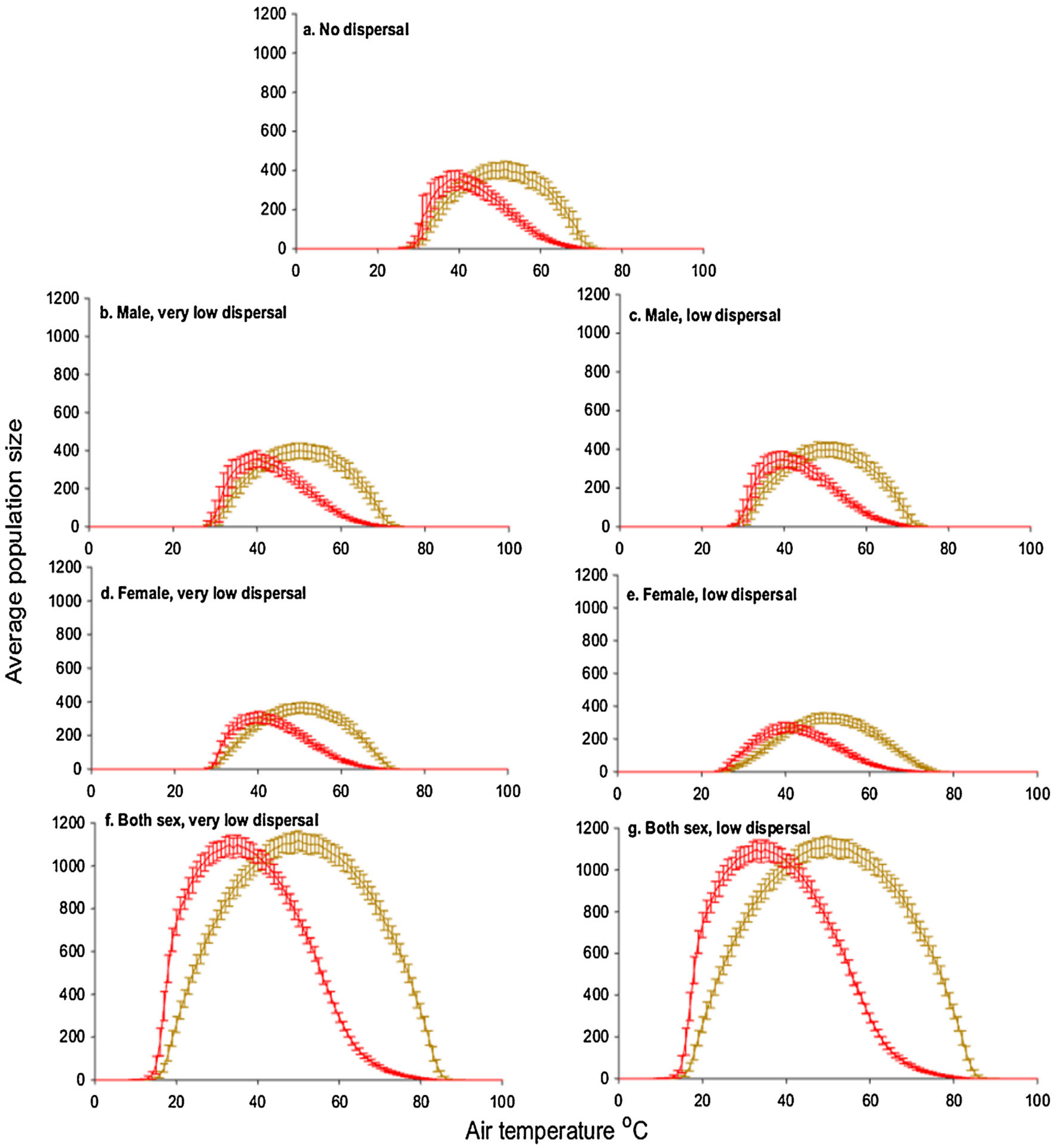

**Fig. 3.** Average population size (±standard errors) against matrix columns 1 to 100 [representing air temperature (°C)] for GSD populations under no climate warming (brown line) and climate warming (red line). The temperature range for no climate warming is 18 to 33 °C and for climate warming is 21 to 36 °C. Each graph shows different combinations of individual sex (male and female) and dispersal tendency, as labelled.

### 2.5. *Dispersal function*

We explored three levels of dispersal ‘none’, ‘low’ and ‘very low’, as there is insufficient empirical data available to accurately parameterise a single dispersal function. Boyle et al. (2014a) also use a ‘large’ dispersal level, but it was not included in this study as many reptile species are considered to disperse relatively small distances (Olsson and Shine, 2003), or do not disperse at all (Escobedo-Galvan et al., 2011). The very low level of dispersal was introduced as it is considered to represent a more realistic level of dispersal for many reptile species (Fig. 2). However, these terms are relative as there are no available data on what ‘low’ or ‘very low’ dispersal would be in these species.

‘Low’ and ‘very low’ levels of dispersal had three separate sex-based tendencies, i.e., male only, female only and dispersal by both sexes. When both sexes dispersed, males and females had equal probabilities of dispersing given by the probability function.

$$Pr\,(\text{dispersal}\quad\text{distance}) = \frac{1}{\left(1 + A * \left(\mathrm{D}_{\mathrm{ij}}^{Z}\right)\right)} \tag{3}$$

Pr(dispersal distance) is the probability that an individual moves a certain distance, $D_{\mathrm{ij}}$, the distance moved between matrix cells (populations). Parameter A defines the distribution of dispersal differences, $1/A$ is the average dispersal distance, and $Z$ is a shape parameter for the dispersal curve (Fig. 2).

### 2.6. *Analysis*

Each simulation was replicated 15 times for each dispersal level (low and very low) and dispersal tendency (none, male, female and

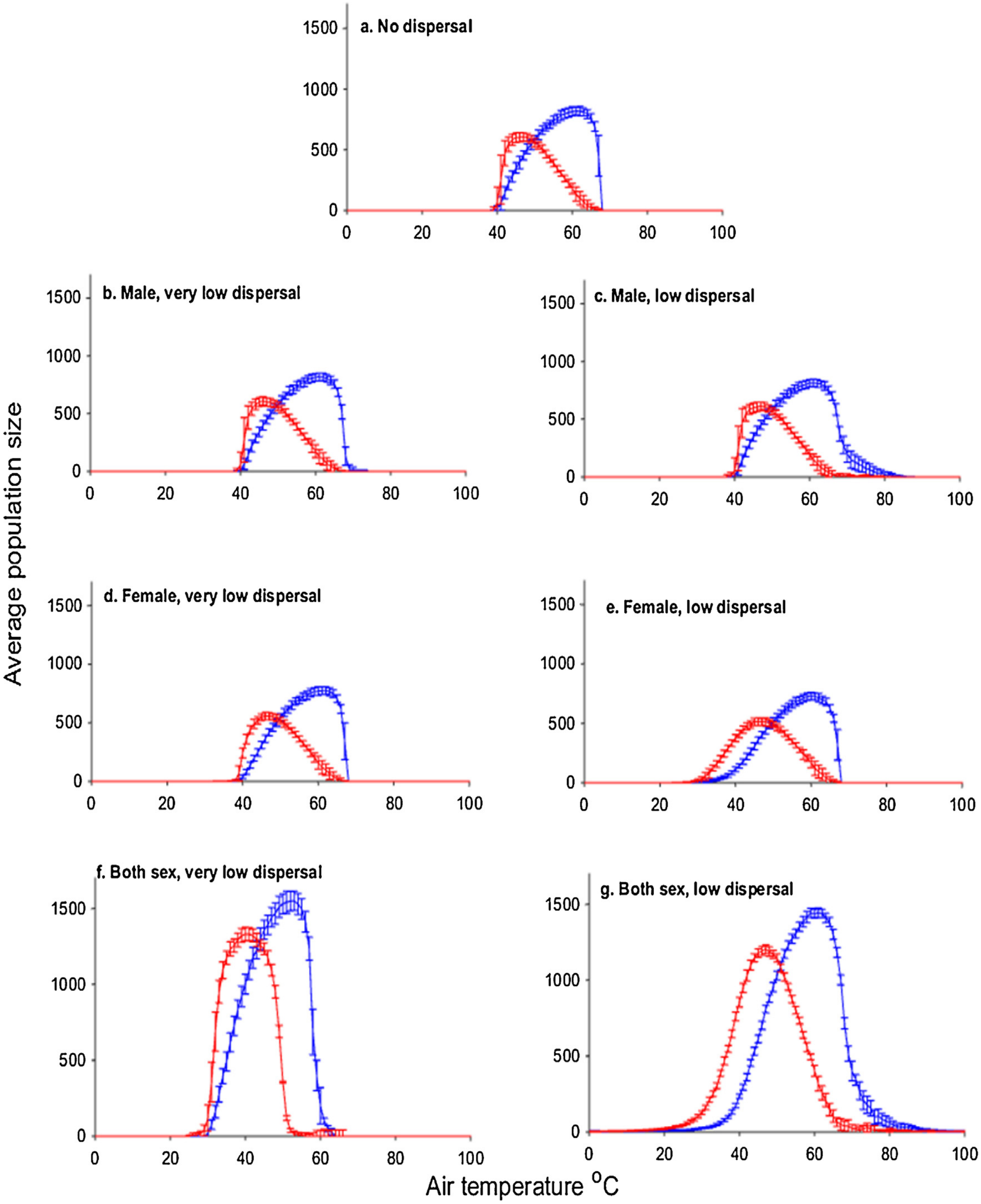

**Fig. 4.** Average population size (±standard errors) against matrix columns 1 to 100 [representing air temperature (°C)] for TSD populations under no climate warming (blue line) and climate warming (red line). The temperature range for no climate warming is 18 to 33 °C and for climate warming is 21 to 36 °C. Each graph shows different combinations of individual sex (male and female) and dispersal tendency, as labelled.

both sexes), for GSD and TSD populations. Population sizes were averaged at each temperature. Temperatures are represented by columns (100 columns, one for each temperature) of the population matrix (Figs. 3 and 4).

## 3. Results

### 3.1. Genotypic sex determination

After 1100 years of simulated stable climatic conditions (Fig. 3, brown lines), and after climate warming (1000 years of simulated stable climatic conditions, followed by 100 years of climate warming) (Fig. 3, red lines), dispersal level (very low or low) did not influence average population size, except when both sexes dispersed (Fig. 3, comparing left and right columns). Without climate warming, populations reached larger sizes (on average) at higher temperatures, compared with climate warming (Fig. 3).

Populations with dispersal by both sexes are much larger on average (Fig. 3f and g) than populations with other dispersal tendencies (Fig. 3a–f). The distributions of populations with climate warming were skewed towards a decrease in average population sizes at the warmer edges of the range (Fig. 3, red lines).

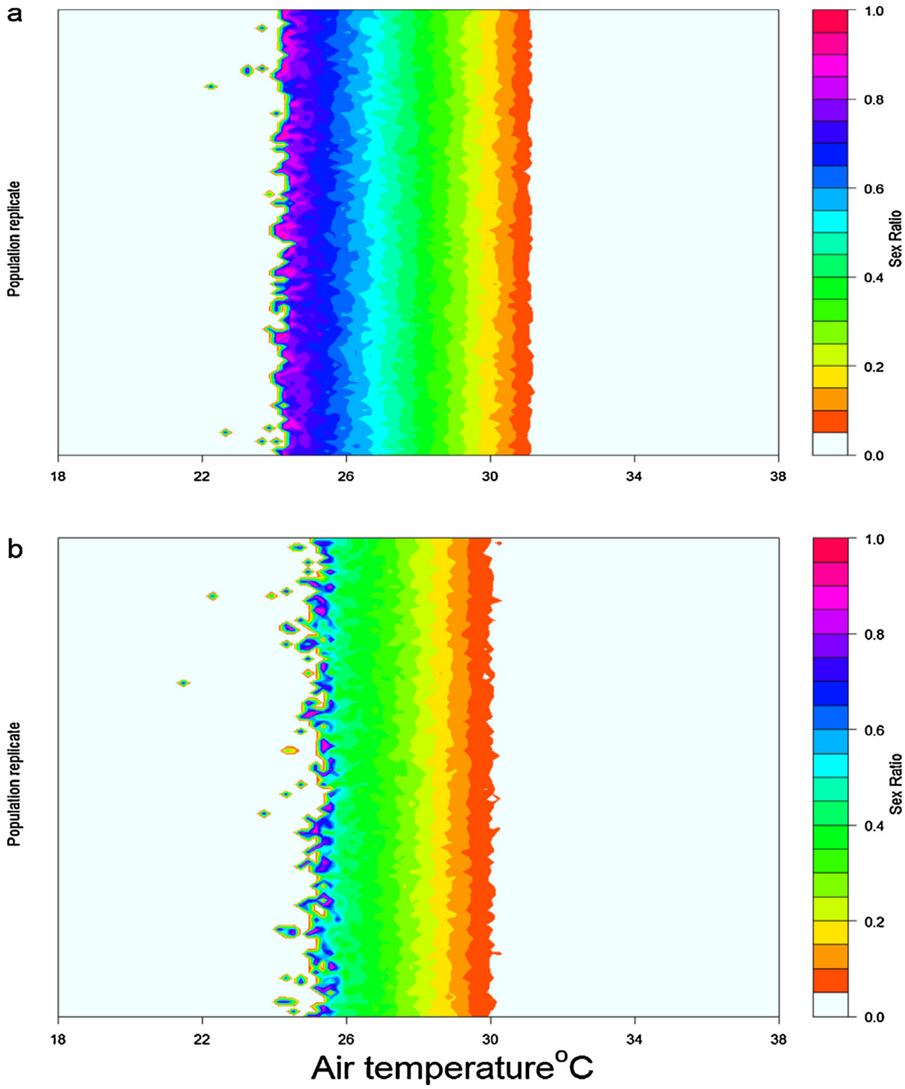

**Fig. 5.** Contour maps of adult sex ratios (proportion male) for TSD populations, with 100 simulation replicates, against environmental temperature (matrix columns 1–100) under (a) no climate warming and (b) climate warming. The pale blue areas represent populations of size zero.

Populations grew to larger sizes at the colder edges of the range (Fig. 3, red lines), compared to those without climate warming (Fig. 3, gold lines).

Dispersal by both sexes resulted in a modest amount of range shift towards the range edge at cold temperatures as climates warmed (Fig. 3f and g). The direction of range shift towards cold temperatures occurs with climate warming (red lines) compared with no climate warming (brown lines) (Fig. 3f and g). Although range contraction at warm range limits was observed, range expansion at the cold range limits was very modest (Fig. 3).

### 3.2. *Temperature-dependent sex determination*

Similar to GSD populations, dispersal level (very low and low) did not seem to influence average population size (Fig. 4, comparing left and right columns) (Spatial representations of these plots for TSD populations with dispersal by both sexes are shown in the supplementary material). But TSD populations (Fig. 4) reached larger average sizes than GSD (Fig. 3) populations. A reduction in average population sizes at the range edge at warm temperatures occurred owing to an increase in female-biased sex ratios and decreased female fecundity where males are limiting. This effect is further exacerbated by climate warming (Fig. 4, red lines). The population distributions became skewed under climate warming, with an overall decrease in average population size at the warmer edge of the range and an increase in population sizes at the cold edge of the range (Fig. 4).

No dispersal (Fig. 4a), male dispersal (Fig. 4b and c) and a very low level of female dispersal (Fig. 4d) resulted in similar population sizes and distributions across ranges without and with climate warming. After climate warming populations with a low level of female dispersal (Fig. 4e, red lines) were more widely distributed across colder edge of the range, but average population sizes were very similar for both dispersal levels (Fig. 4d and e, red lines).

Unsurprisingly, range expansion after climate warming was observed only for species where both sexes dispersed, with notable range expansion when dispersal probabilities were very low (Fig. 4f, columns 25 to 30 are new columns of population occupation with climate warming). Populations with a low level of two-sex dispersal were more widely distributed across the range than with a larger level of dispersal.

Contour maps of the distribution of adult (Fig. 5) and juvenile (Fig. 6) sex ratios with no climate warming and after climate

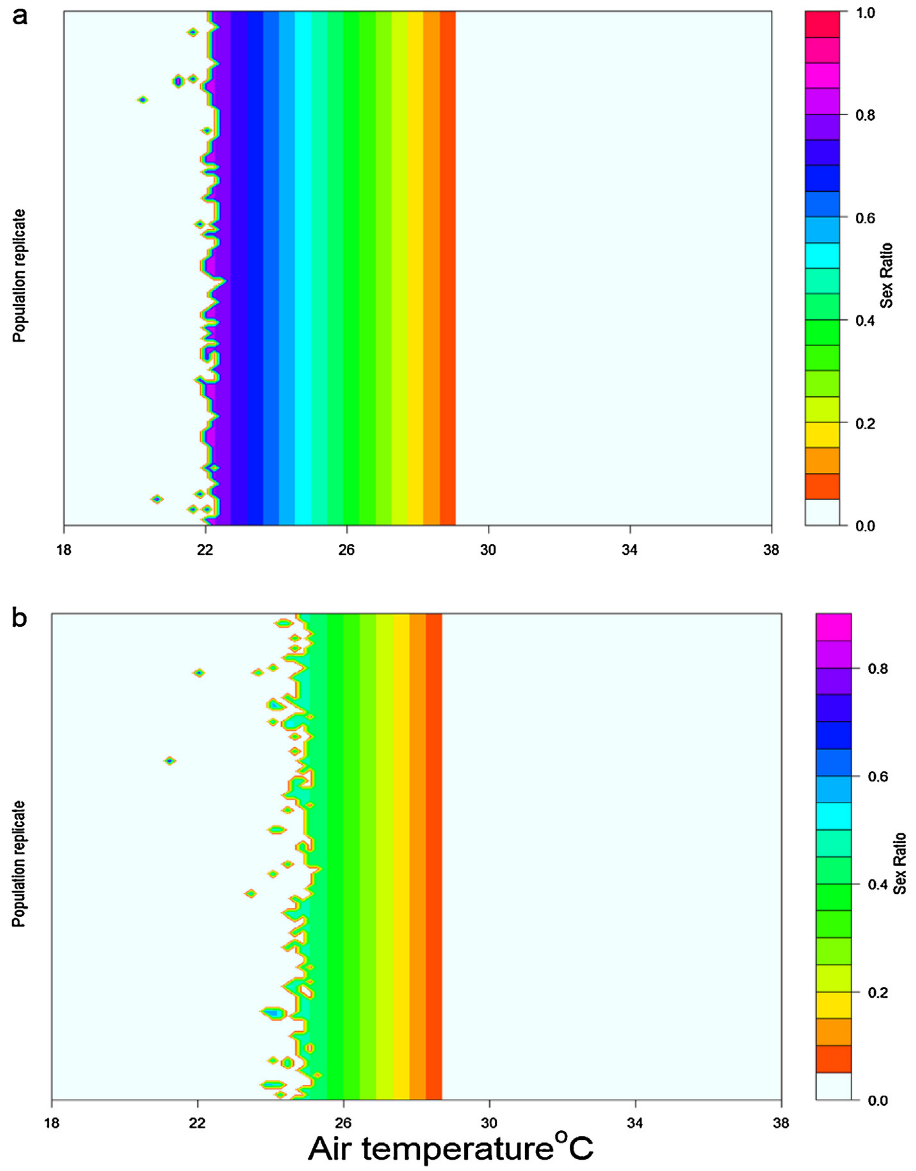

**Fig. 6.** Contour maps of juvenile sex ratios (proportion male) for TSD populations, with 100 simulation replicates, against environmental temperature (matrix columns 1–100) under (a) no climate warming and (b) climate warming. The pale blue areas represent populations of size zero.

warming were produced for TSD reptiles with a very low level of two-sex dispersal (Fig. 4g). Reptiles with a very low level of two-sex dispersal showed some of the largest average population sizes with no climate warming. This corresponds to adult sex ratios of 0.2 to 0.5 (proportion males) (Fig. 5a) and juvenile sex ratios approximately 0.2 to 0.5 (Fig. 6a). Populations changed from even sex ratios without climate warming (Fig. 5a and Fig. 6a), to increasingly female-biased with climate warming (Figs. 5b and 6b). TSD populations without climate warming (Fig. 4f, blue lines, columns 30 to 45) that had male-biased adult sex ratios (Fig. 5a, 0.5 to 0.8, proportion males), grew to larger sizes with climate warming (Fig. 4f, red lines), as the proportion of females in the population increased (Fig. 5b, columns 30 to 45, 0.2 to 0.4, proportion males). Populations declined in the warmest, most female-biased areas (Figs. 4f, red lines, 5b, columns 45 to 50, <0.2 proportion males). After climate warming, populations with even sex ratios or male-biased adult sex ratios had smaller average population sizes than expected compared to the no climate warming scenario (Fig. 7).

## 4. Discussion

There have been numerous predictions that warming climates will skew already biased primary sex ratios of contemporary TSD reptiles towards females resulting in local population extinctions (Hawkes et al., 2007, 2009; Hays et al., 2003; Janzen, 1994; Mitchell and Janzen, 2010; Witt et al., 2010). By contrast some recent studies of sea turtles (e.g. Saba et al., 2012; Laloe et al., 2014) report that rising temperatures may result in an increase in females and consequent population growth, as opposed to decline. More critically, there is a confounding effect of lower juvenile success and survival as temperatures rise (Saba et al., 2012). Adjusting nesting phenology (nesting earlier or later in the year) may affect the rate of juvenile survival. Saba et al. (2012) report that in a leatherback turtle (*Dermochelys coriacea*) population an increase in median nesting date has occurred since the mid-1990s. If turtles nest later in the season, juvenile survival declines owing to warmer and drier conditions. A reduction in juvenile survival owing to rising temperatures may have even more significant consequences for some species

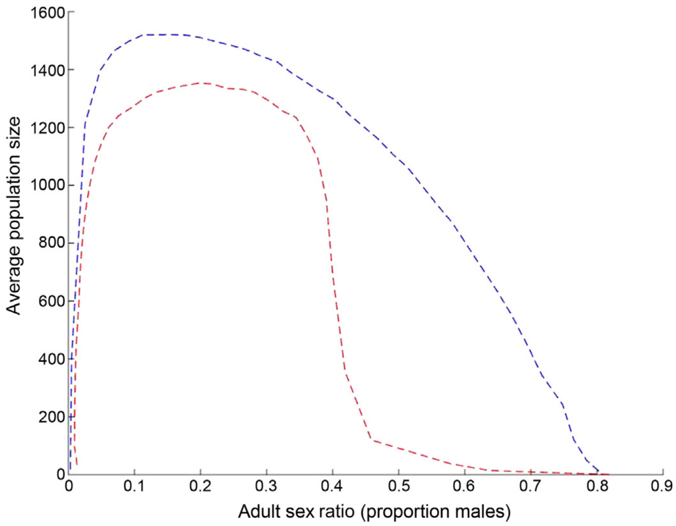

**Fig. 7.** Effect of adult sex ratio (proportion male) on average population size in TSD populations with very low dispersal by both sexes, with no climate warming (blue line) and climate warming (red line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

than increasingly female-biased sex ratios (Saba et al., 2012; Laloe et al., 2014).

Dispersal may be crucial in rescuing TSD reptiles at range margins from local extinction (Boyle et al., 2014a). We showed that the effectiveness of dispersal in determining the extent of range expansion and population persistence in TSD species depends on the level of dispersal and dispersal tendency (Fig. 4). Dispersal tendencies have been quite widely researched in reptiles (Casale et al., 2002; FitzSimmons et al., 1997; Olsson and Shine, 2003; Roberts et al., 2004) and are assumed to enhance population growth and persistence given that dispersal is effective (Doody and Moore, 2011; Kallimanis, 2010). As climates warmed, dispersal had little effect on GSD species (Fig. 3). Dispersal had larger effects on TSD species, enabling greater population sizes, persistence and range expansion than for GSD species (compare Figs. 3 and 4).

A relatively large level of dispersal is needed for sufficient recruitment through immigration so that population numbers do not fall below replacement level, and hence become potential population sinks (Brown and Kodric-Brown, 1977; Krebs, 2009). Dispersal among populations may bring the rare sex into sex-biased populations, rescuing them from demographic collapse, and may lead to wider ranges (Boyle et al., 2014a). For reptiles with TSD pattern 1B (males produced at higher temperatures, e.g. the tuatara) as temperatures rise, females become the rare sex. Even if dispersal by females occurred it may not facilitate successful reproduction owing to male aggression in competing for females. We showed that after climate warming dispersal was only observed in one instance to lead to notable range expansion (Figs. 4f and 5b).

The specification that the population matrix has an edge is an analytical limitation of our model, making it difficult to determine relative dispersal levels, i.e., low and very low, with accuracy. Evidence from field based studies suggests that, some terrestrial (Olsson and Shine, 2003) and aquatic (Brown and Brooks, 1993; Mockford et al., 2005; Morreale et al., 1984) reptiles may only disperse distances up to a few metres and many reptiles do not disperse (Escobedo-Galvan et al., 2011). Marine turtles are known to be very effective dispersers, and males may disperse across entire oceans for reproductive opportunities (Casale et al., 2002; Roberts et al., 2004; Wright et al., 2012). Nevertheless, for many other reptile species it is not known how far they extend their ranges through dispersal.

Our findings on population growth are consistent with the predictions of Kallimanis (2010), of population decrease at the warmer (trailing) edge of the range, and population increase at the colder (leading) edge of the range, as climates warm. However, the explanations for population growth at the colder edge of the range differed from the predictions of Kallimanis (2010) of sex ratios becoming even as climates warmed, resulting in rapid population growth. We found that increasingly female-biased sex ratios, rather than even sex ratios, led to larger population sizes as climates warmed by 3 °C (Figs. 5 and 6). TSD species located at the colder edge of the range that had male-biased or even sex ratios (Figs. 4, blue lines, 5a and 6a), increased to large sizes as the proportion of females in the population increased with climate warming (Figs. 4, red lines, 5b and 6b).

Populations declined at the warmest, most female-biased part of the range, as accompanying an increase in the number of females was a decrease in the number of males produced and recruited, and a decrease in juvenile survival (Fig. 4). Estimations of the adult sex ratios (Fig. 5) and juvenile sex ratios (Fig. 6) revealed that increasingly female-biased adult (and juvenile) sex ratios resulted in population growth at the colder edge of the range, as climates warmed. This is consistent with the findings of Freedberg and Taylor (2007) that female-biased, and not even, sex ratios will lead to rapid population growth, following climate warming (Boyle et al., 2014a; Freedberg and Taylor, 2007).

Climate warming is predicted to result in the creation of new and more favourable habitats in previously cold areas (Kallimanis, 2010). Consequent population growth will result in a new pool of dispersers to colonise newly created habitats. This in turn will facilitate range expansion. Our findings differed in relation to range expansion. While range contractions occurred in both GSD (Fig. 3) and TSD (Fig. 4) species, range expansion at the colder edge of the range was very modest (e.g. Fig. 4f). In contrast with Kallimanis (2010), we found that range expansion following climate warming occurred when sex ratios were male-biased and not even (comparing Figs. 3f and 4f). Furthermore, range expansion following climate warming resulted in populations that were largely male-biased and had smaller average sizes (Figs. 5b and 6b).

Escobedo-Galvan et al. (2011) criticised the model of Kallimanis (2010) as an oversimplification of the processes involved in the response of TSD species to climate change. The model proposed by Kallimanis (2010) considers only the effects of temperature on biased sex ratios, and assumes that dispersal is effective. We showed that temperature effects on survival are also important for range shift. Furthermore, dispersal is not necessarily effective, and is influenced by many factors, including dispersal scenario. The successful continuation of TSD populations has been argued to rely on male recruitment and dispersal to facilitate population persistence in female-biased populations as climates warm (Doody and Moore, 2011). Assuming that dispersal is effective in reptile species, a low level of male (Fig. 4c) and female (Fig. 4e) dispersal facilitated population persistence, at the warmer and colder edges of the range, respectively and without climate warming (Boyle et al., 2014a). Female dispersal has been reported by only one study (Olsson and Shine, 2003).

As climates warmed, the primary sex ratios of TSD populations became more female-biased and combined with lower male densities, meant that fewer males were produced and dispersed. If males dispersed too far along the warmer edge of the temperature range they would encounter fewer surviving females (Boyle et al., 2014a). If females dispersed and males remained in their home ranges then males incurred no additional cost of dispersal related mortality. There were many more females produced than males in a warming climate for low dispersal in TSD populations. A large number of females dispersing, or dispersing greater distances towards the colder edges of the ranges, were more likely to encounter surviving males, increasing population persistence (Boyle et al., 2014a).

Male dispersal is thought to be the dominant dispersal tendency in reptiles. Studies of gene flow and dispersal between populations are based primarily on research in marine turtles (Karl et al., 1992; Casale et al., 2002; Roberts et al., 2004; Bowen and Karl, 2007). In marine turtles, males are excellent dispersers (Roberts et al., 2004), but there is a lack of information about dispersal tendencies or success for most other TSD species (Olsson and Shine, 2003). Indeed, Escobedo-Galvan et al. (2011) argue that many TSD species are poor dispersers. Notwithstanding, many TSD species are not only facing the impacts of human-induced climate warming and, hence, biased offspring sex ratios (Hawkes et al., 2009; Hays et al., 2003; Janzen, 1994), but also habitat destruction and fragmentation. This in turn may lead to a reduction in the number of nesting sites for females, reproductive rates, dispersal and potential for range expansion to offset the effects of climate warming (Parmesan et al., 2000; Poloczanska et al., 2009; Fuentes et al., 2011).

Wedekind (2002) demonstrated that female-biased sex ratios result in larger population sizes, given that there are at least some males, and this is consistent with our results of maximum average populations size coinciding with an adult sex ratio of 0.2 (proportion males) (Fig. 7) (Wedekind, 2002). Following climate warming population sizes declined dramatically in populations with male-biased or equal sex ratios (Fig. 7). This is because before climate warming most populations of non-zero size had adult sex ratios of 0.2 to 0.8 (proportion male), and following climate warming populations had adult sex ratios of 0.05 to 0.4 (proportion males). So essentially there were few populations remaining with male-biased or equal sex ratios, with climate warming (Fig. 7).

## 5. Conclusions

Dispersal influenced range shift after climate warming to a greater extent in TSD than in GSD species. Range expansion into colder areas was only notable in TSD reptiles with a very low level of dispersal by both sexes. Dispersal by individuals of the rare sex is more essential in maintaining populations of TSD reptiles. Dispersal of the rare sex enables them to mix with the opposite sex located towards either the warmer or colder range edges in stable climates (Boyle et al., 2014a). Our novel finding is that biased sex ratios are more likely to influence range expansion than even sex ratios, but only when dispersal by both sexes occurs. Our results suggest that if faced with climate warming of 3 °C over the next 100 years (IPCC, 2013) TSD reptiles will be vulnerable to reductions in population growth and persistence, at the warmer edge of their range, and show limited capacity for range expansion.

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## References

Bowen, B., Karl, S., 2007. Population genetics and phylogeography of sea turtles. Mol. Ecol. 16, 4886–4907.

Boyle, M., Schwanz, L.E., Hone, J., Georges, A., 2014a. How do climate-linked sex ratios and dispersal limit range boundaries? BMC Ecol. 14, 1–10.

Boyle, M., Hone, J., Schwanz, L., Georges, A., 2014b. Under what conditions do climate-driven sex ratios enhance versus diminish population persistence? Ecol. Evol. 4, 4525–4535.

Brown, G.P., Brooks, R.J., 1993. Sexual and seasonal differences in activity in a northern population of snapping turtles, *Chelydra serpentina*. Herpetologica 49, 311–318.

Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58, 445–449.

Casale, P., Laurent, L., Gerosa, G., Argano, R., 2002. Molecular evidence of male-biased dispersal in loggerhead turtle juveniles. J. Exp. Mar. Biol. Ecol. 267, 139–145.

Doody, J.S., Moore, J.A., 2011. Conceptual model for thermal limits on the distribution of reptiles. Herpetol. Conserv. Biol. 5, 283–289.

Escobedo-Galvan, A.H., Gonzalez-Salazar, C., Lopez-Alcaide, S., Arroyo-Pena, V.B., Martinez-Meyer, E., 2011. Will all species with temperature-dependent sex determination respond the same way to climate change? A reply to Kallimanis (2010). Oikos 120, 795–799.

Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Oxford University Press, Oxford.

FitzSimmons, N.N., Moritz, C., Limpus, C.J., Pope, L., Prince, R., 1997. Geographic structure of mitochondrial and nuclear gene polymorphisms in Australian green turtle populations and male-biased gene flow. Genetics 147, 1843–1854.

Freedberg, S., Taylor, D.R., 2007. Sex ratio variance and the maintenance of environmental sex determination. J. Evol. Biol. 20, 213–220.

Fuentes, M., Limpus, C.J., Hamann, M., 2011. Vulnerability of sea turtle nesting grounds to climate change. Global Change Biol. 17, 140–153.

Gibbons, J.W., Novak, S.S., Ernst, C.H., 1988. *Chelydra serpentina* (Linneaus), snapping turtle. Cat. Am. Amphib. Reptiles 420, 1–4.

Grayson, K.L., Mitchell, N.J., Monks, J.M., Keall, S.N., Wilson, J.N., Nelson, N.J., 2014. Sex ratio bias and extinction risk in an isolated population of tuatara (*Sphenodon punctatus*). PLoS ONE 9, e94214.

Harts, A.M.F., Schwanz, L.E., Kokko, H., 2014. Demography can favour female-advantageous alleles. Proc. R. Soc., B:Biol. Sci. 281, 1790.

Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2007. Investigating the potential impacts of climate change on a marine turtle population. Global Change Biol. 13, 923–932.

Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2009. Climate change and marine turtles. Endangered Species Res. 7, 137–154.

Hays, G.C., Broderick, A.C., Glen, F., Godley, B.J., 2003. Climate change and sea turtles: a 150-year reconstruction of incubation temperatures at a major marine turtle rookery. Global Change Biol. 9, 642–646.

Holleley, C., O'Meally, D., Sarre, S.D., Marshall Graves, J.A., Ezaz, T., Matsubara, K., Azad, B., Zhang, X., Georges, A., 2015. Sex reversal triggers the rapid evolution of temperature dependent sex. Nature 523, 79–82.

Hughes, L., 2003. Climate change and Australia: trends, projections and impacts. Aust. Ecol. 28, 423–443.

IPCC, 2013. Climate change 2013: the physical basis. In: Contribution of Working Group I to the Fifth Assessment. Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

Janzen, F.J., 1994. Climate change and temperature-dependent sex determination in reptiles. Proc. Natl. Acad. Sci. U.S.A. 91, 7487–7490.

Kallimanis, A.S., 2010. Temperature dependent sex determination and climate change. Oikos 119, 197–200.

Karl, S.A., Bowen, B.W., Avise, J.C., 1992. Global population genetic structure and male-mediated gene flow in the green turtle (*Chelonia mydas*): RFLP analyses of anonymous nuclear loci. Genetics 131, 163–173.

Krebs, C.J., 2009. Ecology. The Experimental Analysis of Distribution and Abundance, sixth ed. Benjamin Cummings, New York, NY.

Laloe, J.-O., Cozens, J., Renom, B., Taxonera, A., Hays, G.C., 2014. Effects of rising temperature on the viability of an important sea turtle rookery. Nat. Clim. Change 4, 513–518.

McGaugh, S.E., Janzen, F.J., 2011. Effective heritability of targets of sex-ratio selection under environmental sex determination. J. Evol. Biol. 24, 784–794.

Mitchell, N.J., Kearney, M.R., Nelson, N.J., Porter, W.P., 2008. Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? Proc. R. Soc., B:Biol. Sci. 275, 2185–2193.

Mitchell, N.J., Janzen, F.J., 2010. Temperature-dependent sex determination and contemporary climate change. Sex. Dev. 4, 129–140.

Mockford, S.W., McEachern, L., Herman, T.B., Synder, M., Wright, J.M., 2005. Population genetic structure of a disjunct population of Blanding's turtle (*Emydoidea blandingii*) in Nova Scotia, Canada. Biol. Conserv. 123, 373–380.

Morjan, C.L., 2003. How rapidly can maternal behaviour affecting primary sex ratio evolve in a reptile with environmental sex determination? Am. Nat. 162, 205–219.

Morreale, S.J., Gibbons, J.W., Congdon, J.D., 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). Can. J. Zool. 62, 1038–1042.

Olsson, M., Shine, R., 2003. Female-biased natal and breeding dispersal in an alpine lizard, *Niveoscincus microlepidotus*. Biol. J. Linn. Soc. 79, 277–283.

Parmesan, C., Root, T.L., Willig, M.R., 2000. Impacts of extreme weather and climate on terrestrial biota. Bull. Am. Meteorol. Soc. 81, 443–450.

Poloczanska, E.S., Limpus, C.J., Hays, G.C., 2009. Vulnerability of marine turtles to climate change. Adv. Mar. Biol. 56, 151–211.

Rankin, D.J., Kokko, H., 2007. Do males matter? The role of males in population dynamics. Oikos 116, 335–348.

Roberts, M.A., Schwartz, T.S., Karl, S.A., 2004. Global population genetic structure and male-mediated gene flow in the green sea turtle (*Chelonia mydas*): analysis of microsatellite loci. Genetics 166, 1857–1870.

Saba, V.S., Stock, C.A., Spotila, J.R., Paladino, F.V., Tomillo, P.S., 2012. Projected response of an endangered marine turtle population to climate change. Nat. Clim. Change 2, 814–820.

Schwanz, L.E., Janzen, F.J., Proulx, S.R., 2010. Sex allocation based on relative and absolute condition. Evolution 64, 1331–1345.

Silber, S., Geisler, J.H., Bolortsetseg, M., 2011. Unexpected resilience of species with temperature-dependent sex determination at the Cretaceous–Paleogene boundary. Biol. Lett. 7, 295–298.

Warner, D.A., Shine, R., 2008. The adaptive significance of temperature-dependent sex determination in a reptile. Nature 451, 566–568.

Wedekind, C., 2002. Manipulating sex ratios for conservation: short-term risks and long-term benefits. Anim. Conserv. 5, 13–20.

Witt, M.J., Hawkes, L.A., Godfrey, M.H., Godley, B.J., Broderick, A.C., 2010. Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle. J. Exp. Biol. 213, 901–911.

Wright, L.I., Stokes, K.L., Fuller, W.J., Godley, B.J., McGowan, A., Snape, R., Tregenza, T., Broderick, A.C., 2012. Turtle mating patterns buffer against disruptive effects of climate change. Proc. R. Soc. London, Ser. B 279, 2122–2127.

Yntema, C.L., Mrosovsky, N., 1982. Critical periods and pivotal temperatures for sexual-differentiation in loggerhead sea turtles. Can. J. Zool. 60, 1012–1016.